

Developing and testing a landscape-scale habitat suitability model for fisher (*Martes pennanti*) in forests of interior northern California

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ABSTRACT

The fisher is warranted for protection under the Endangered Species Act in the western United States and, as such, it is especially important that conservation and management actions are based on sound scientific information. We developed a landscape-scale suitability model for interior northern California to predict the probability of detecting fishers and to identify areas of important fisher habitat. Previous models have been extrapolated to this region, but our model was developed from the results of strategically planned detection surveys within the study area. We used generalized additive modeling to create a model that best distinguished detection ($n=55$) from non-detection ($n=90$) locations on the basis of environmental covariates. Four models were averaged to create a final model including the following variables: Amount of Dense Forest, Percent Hardwood, Medium & Large Trees, Structurally Complex Forest, Adjusted Elevation, Insolation Index and Predicted Abundance of Mammalian Prey. This model was well calibrated and correctly classified fisher detections 83.6% of the time and absences (non-detections) 70.0%. Independent test data were classified less well; 76.2% and 53.0%, respectively, perhaps a result of differences in the spatial and temporal characteristics of the data used to build versus test the model. The model is the first comprehensive portrayal of the distribution and configuration of habitat suitability in this region and provides managers a tool to monitor habitat change over time and to plan vegetation treatments. It also represents an example for the development of similar models for dispersal-limited mammals with large area needs, as well as other species associated with late-successional forests in northern California.

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1. Introduction

Models that predict species distributions can help understand ecological requirements and assist in conservation planning (Guisan and Zimmerman, 2000; Pearce and Boyce, 2006; Scott et al., 2002; Guisan and Thuiller, 2005; Kearney, 2006; Zielinski et al., 2006a). Regional landscape-scale suitability models statistically relate field survey results to a set of environmental characteristics. These characteristics are presumed to directly influence elements of the species' niche, or correlate with such elements. The output from such models, which are typically in the form of a map of predicted occurrence or predicted habitat suitability (Hirzel et al., 2006), estimate the probability of finding a species in areas that have not been surveyed. These features make it possible to compare the predicted probability of occurrence or habitat suit-

ability among land ownership types (e.g., Carroll and Johnson, 2008), to identify unoccupied but apparently suitable areas for reintroduction (Carroll et al., 2003; Seddon et al., 2007), to compare habitat suitabilities among species (Zielinski et al., 2006a; Carroll et al., in press) and other applications for conservation planning. Ultimately we can only understand niche relations, and identify limiting resources, through experimentation and long-term demographic studies (Austin, 1985; Anthony et al., 2006). In the absence of such studies, however, empirically based statistical models of species-environment associations provide landscape-scale inferences that can assist in immediate conservation planning needs.

In the western U.S., the fisher occurred historically throughout the northern Rocky Mountains, Cascade and Coast Ranges and the Sierra Nevada (Gibilisco, 1994). The range and abundance of this forest-dwelling carnivore have decreased dramatically in the West due to commercial trapping, changes in forest structure associated with logging and altered fire regimes, increased human access, and habitat loss to urban and recreational devel-

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opment (Powell and Zielinski, 1994; Zielinski et al., 2005). The fisher occupies less than half of its historical range, as described in the early 1900s (Grinnell et al., 1937), and remnant populations in the southern Sierra Nevada are separated by >400 km from the nearest populations in northern California (Zielinski et al., 1995; Carroll et al., 1999). Population decline and fragmentation in the Pacific states has reduced genetic diversity (Drew et al., 2003) and the fisher was deemed “warranted but precluded” for listing under the Endangered Species Act (U.S. Fish and Wildlife Service, 2004). Quantitative predictive mapping of habitat suitability will support future determinations of the regulatory status of the fisher, enable evaluation of potential impacts of land management activities, assist in planning reintroductions, and help identify important habitat conditions for fishers.

The fisher has been the subject of a number of previous landscape-scale habitat modeling efforts in California. It is easily detected using noninvasive survey methods (remote cameras: Kays and Slauson, 2008, track-plate stations: Ray and Zielinski, 2008) and these methods have been used in standard protocols (Zielinski and Kucera, 1995; Zielinski et al., 2005) to generate systematically collected, independently verifiable (McKelvey et al., 2008) and spatially precise survey data. Resulting data on the detections and non-detections have been used to build statistical landscape-scale habitat models for the fisher in northwestern California (Carroll et al., 1999; Davis et al., 2007), portions of the Sierra Nevada (Campbell, 2004; Davis et al., 2007; Spencer et al., in press) and statewide (Davis et al., 2007).

A predictive landscape habitat model for the fisher developed specifically for interior northern California in the eastern Klamath Mountains region is currently lacking. Unlike other regions of California (e.g., Zielinski et al., 2005), prior to our work there was no systematically collected survey data for the majority of our study region. Nonetheless, predictions for the western portion of our study region were derived from a habitat modeling exercise in northwestern California (Carroll et al., 1999) and predictions for the entire study region were derived from characteristics associated with fisher detections elsewhere (Davis et al., 2007). However, characteristics of fisher habitat, diet and genetics, vary substantially in different parts of the state (Zielinski et al., 1999, 2004a,b; Wisely et al., 2004; Golightly et al., 2006; Davis et al., 2007). The poor performance of a landscape habitat model for the southern Sierra Nevada at predicting fisher detections in northern California and vice versa (Davis et al., 2007) demonstrates the need to develop and test specific models for the Klamath region. Moreover, fisher habitat in the more western coastal forests is predicted by spatial phenomena related to east–west precipitation gradients and geographic predictors (Carroll et al., 1999); thus, extrapolating that model to our study area would not be appropriate.

Here, we report a new landscape-scale habitat suitability model (hereafter landscape habitat model) for the fisher in north-central California that we test with an independent data set. We use a systematic survey approach that provides an unbiased sample from various land ownerships in the study area. Unlike previous large-scale survey and modeling efforts for the fisher in California, which were conducted primarily on public land, this is also the first regional fisher sampling effort to deliberately seek inclusion of non-federal lands. Because conservation decisions can be based on such predictive models, incorporating lands with a more complete range of past and current management objectives and practices is needed to fully understand the relationships between fisher occurrence and environmental characteristics. We evaluate the validity of our model using independent data and conclude by offering suggestions for potential applications of the model in both management and conservation contexts.

2. Methods

2.1. Study area

The 2,145,000 ha study area was primarily forested land in Del Norte, Humboldt, Siskiyou, Trinity and Shasta Counties, California (Fig. 1). Public land represents 1,502,000 ha (70%) of the area of which 52% is wilderness and Late-Successional Reserves (a special designation under the Northwest Forest Plan [USDA and USDI, 1994] a bioregional conservation plan that applies to federal lands within the study area). Private land, where the dominant land use is commercial forestry, comprises 642,600 ha (30%). Climatic conditions change from wetter to drier and to more variable temperatures when moving from northwest to southeast. Average annual precipitation ranges from 46 to 305 cm a year (Miles and Goudey, 1997). Elevation ranges from 71 to 4350 m with persistent snow typically occurring above ~1500 m during the winter. Douglas-fir (*Pseudotsuga menziesii*)/mixed evergreen-hardwood is the most extensive forest type in the Klamath region with white and red fir (*Abies concolor* and *Abies magnifica*, respectively) found at higher elevations (Sawyer and Thornburgh, 1977). In the eastern portion of the study area, where it joins with the Cascade Range, there are more xeric forest types which are dominated by pine (*Pinus ponderosa* and *Pinus sabiniana*) and deciduous oaks (*Quercus garryana* and *Quercus kelloggii*).

2.2. Fisher survey data

The survey data (Fig. 1) came from three sources: (1) new field surveys, primarily in the center of the study area, conducted in 2005 and 2006 ($n=66$ sample units), (2) surveys on the eastern margin of the study area that were conducted in 2002 as part of a previous study (Davis et al., 2007) ($n=21$ sample units), and (3) surveys on the western margin of the study area that were conducted in 1996–1997 that were also part of a previous study (Carroll et al., 1999) ($n=58$ sample units). Twenty-eight (19.3%) of the sample units were on private land. All surveys ($n=145$ sample units) used a pre-existing national systematic sampling grid (based on the Forest Inventory and Analysis [FIA] system; Bechtold and Patterson, 2005) as the basis for selecting sample units. The FIA grid is a contiguous lattice of hexagonal cells, each approximately 2430 ha in size (see Bechtold and Patterson, 2005 for details), but we included in our sample only every other hexagon in each east–west row within the lattice. Because of the offset nature of the hexagons among rows, this resulted in a sample grid of approximately 10.9 km spacing between points within the same row and 7.7 km spacing between the nearest sample points on adjacent rows. This spacing was chosen on the basis of average fisher home range sizes in California (Zielinski et al., 2004b) to minimize the possibility that the same fisher would be detected at more than 1 sample unit.

We were unable to conduct surveys at all the sample units we originally identified within our study area. Reasons for exclusion included: safety concerns, accessibility, location in unsuitable areas, and strategic choices due to limited funding. At each selected hexagon we established a sample unit composed of six sooted and baited enclosed track-plate stations. A track-plate station was placed as close as possible to the FIA grid cell's center, and the remaining five stations were positioned at 72° intervals approximately 500 m from the center station (Zielinski et al., 2005). The track plate consisted of an aluminum plate (20 cm × 76.2 cm × 0.1 cm). The half of the plate closest to the opening was sooted with either carbon from an acetylene torch or photocopier toner ink (Belant, 2003), and the remainder was covered with white contact paper and enclosed in a box made of corrugated plastic. The track-plate station was baited with raw chicken at each visit and a scent lure (Gusto,

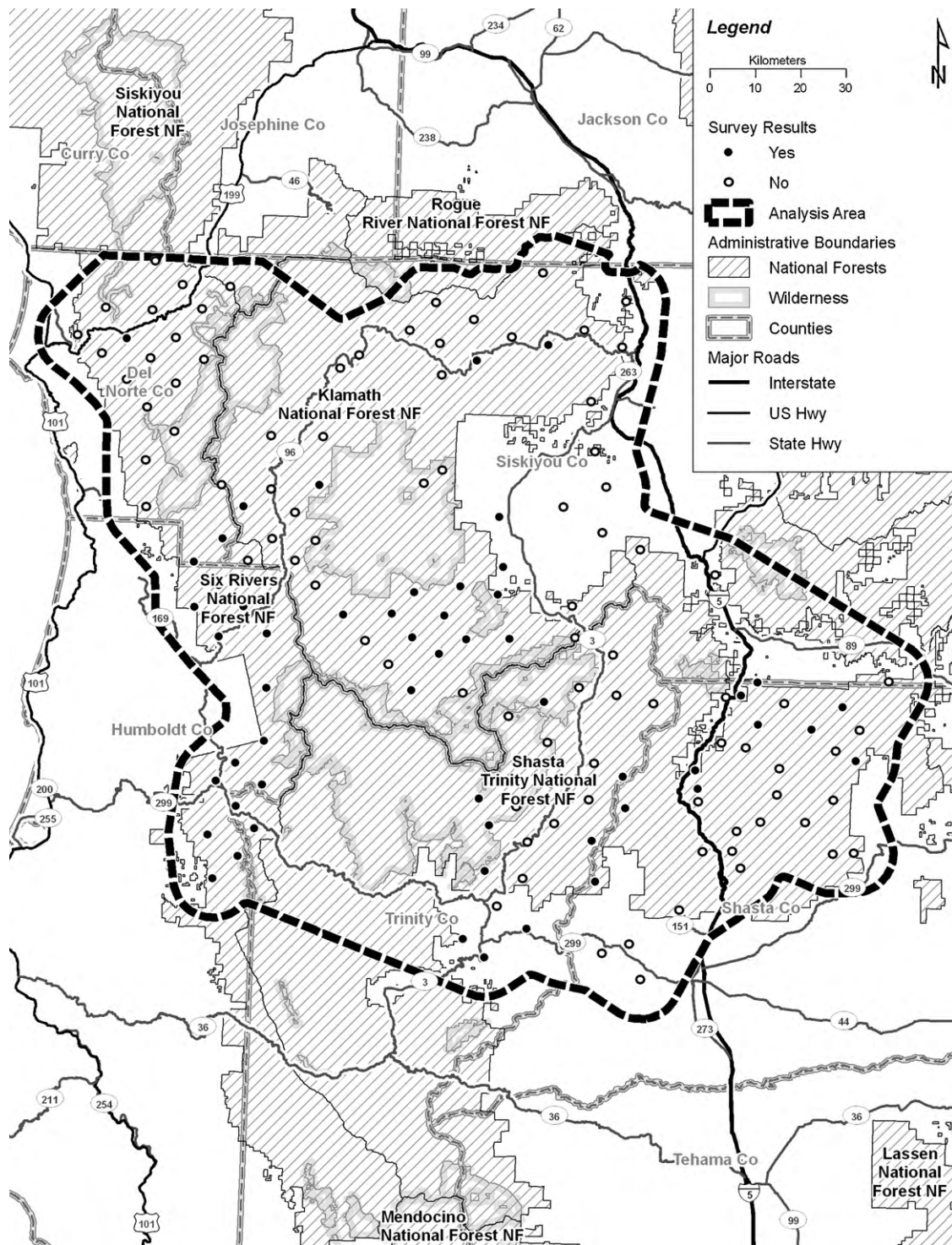


Fig. 1. The study area, in interior northern California (dotted line), and the sample units that detected (black circles) and did not detect (white circles) a fisher during a 16-day survey period.

Minnesota Trapline Products, Pennock, MN, USA) on the 1st and the 5th visits to each station. Field crews returned to check and rebait the track stations at 2-day intervals during a 16-day sampling period, for a total of 8 visits. The tracks of most species detected were distinguished by species-specific characteristics of their tracks (Taylor and Raphael, 1988; Zielinski and Truex, 1995) and the use of a voucher collection of reference tracks (<http://www.fs.fed.us/psw/topics/wildlife/mammal/tracks.shtml>). Most sampling (68%) was conducted between 1 June and 1 Novem-

ber. A verified fisher detection at any of the six track-plate stations in the sample unit, and during any of the eight sampling occasions, resulted in "fisher detected" being recorded for that sample unit.

2.3. Environmental predictor variables

We considered 11 categories of landscape-scale predictor variables: climate, topography, linear features (roads and streams), vegetation cover type, classified habitat type (California Wildlife

Habitat Relationships [CWHR] system; California Department of Fish and Game 1992), vegetation density, tree size class, landscape arrangement, landscape diversity, disturbance and potential mammalian prey habitat (Appendix A). We assessed all predictor variables at a 100 m (1 ha) pixel size within a 5 km² circular moving window centered on each pixel in the study area.

We derived climatic variables from PRISM 800-m gridded data for mean monthly and annual precipitation and mean daily temperature for the period 1971–2000, resampled to 100-m pixels (PRISM Climate Group, <http://www.prismclimate.org>). We derived snow data from SNODAS (Snow Data Assimilation System; National Snow and Ice Data Center) as mean maximum daily snow depth for the period of January–March, 2005. We derived topographic variables from USGS NHDPlus 30-m gridded digital elevation data resampled to 100 m (NHDPlus; a version of the National Elevation Dataset). Variables derived from elevation data include latitude-adjusted elevation (Schoenherr, 1992), topographic relief, southwest exposure index (Franklin, 2003), mean solar insolation index (Gustafson et al., 2003), and aspect 225 (proportion of local landscape with an aspect of 180–270°).

We derived roads primarily from USDA Forest Service Region 5 (California) Northwest Forest Plan (NWFP; USDA and USDI, 1994) transportation data, compiled from travel-routes data for all California national forests within the NWFP region. We derived perennial stream density from compiled National Hydrography Dataset High Resolution data. Both road and stream densities were represented as km/km² within the 5-km² moving window.

We derived landscape-scale vegetation variables from USDA Forest Service Existing Vegetation (EVEG) data (USDA, 2007; <http://www.fs.fed.us/r5/rs/clearinghouse/cite.shtml>). Approximately 90% of the study area includes EVEG data that was updated in 2003 or 2004; the balance was updated from 1998 to 1999. Thus, the vegetation data available for prediction have roughly the same temporal characteristics as the fisher survey data. We extracted cover type, tree size class and vegetation density class variables from EVEG as the proportion of pixels within the 5-km² moving window that met the criteria for each variable within these classes.

We also used EVEG vegetation data to generate a CWHR fisher habitat suitability rating. Based on expert judgment, CWHR rates the suitability of each combination of cover type, canopy closure class, and tree size class as high (1.0), medium (0.66), low (0.33), or unsuitable (0), and calculates an overall habitat suitability rating based on the mean of the separate scores for 'reproduction', 'cover' and 'feeding'. Like others before us (Davis et al., 2007), we believe that current CWHR system was in error in assigning high suitability scores to some forest types, consequently we modified the ratings to create "CWHR2" scores (Appendix A).

The landscape arrangement of vegetation types was calculated by evaluating patch sizes, perimeter–area ratios and nearest neighbor distances within the 5-km² moving window: (1) for CWHR vegetation types classified as high reproductive value and (2) to distinguish CWHR patches with habitat scores > 0 from those with habitat value = 0 (Appendix A). Landscape arrangement variables were derived using FRAGSTATS (McGarigal et al., 2002).

California fishers have a broad diet that includes a wide variety of animal prey, fruit, and insects (Zielinski et al., 1999; Golightly et al., 2006). Landscape diversity was a category of predictor variables intended to reflect plant community diversity, which in turn may represent the diversity of prey available to fishers. The diversity of CWHR vegetation classes, and combinations therein, within each 5-km² moving window, were represented using the Shannon Diversity index (Shannon and Weaver, 1949). We also attempted to represent the relative importance of fisher prey more directly, by using the CWHR system to determine the relative value of habitat for mammalian prey species within 5-km² moving windows areas. Using information about the fisher diet in northwestern California

(Golightly et al., 2006), we created two variables to index the potential abundance of dominant mammalian prey (mammals constitute most of the dietary items in northwestern California; Golightly et al., 2006). We summarized the composite habitat value for "common" mammalian prey (>5% frequency in diet; MAMMPREY, see Appendix A for details) as well as the habitat value for "big" mammalian prey (>0.25 kg and >5% frequency in diet; BIGMAMMPREY, see Appendix A).

Disturbance was represented by the amount of tree plantations, as an indication of recent clear-cut timber harvest, and wild fires (pre-1990 fires distinguished from fires from 1990 to 2005; Appendix A) within the 5-km² moving window areas.

2.4. Modeling approach and statistical analysis

We used non-parametric logistic regression, a subset of Generalized Additive Models, with loess smoothing functions (Cleveland, 1985) to model the relationship between detection and non-detection of fishers at each sample unit and the environmental variables described above. Each sample unit was geo-referenced at the center track-plate station. The probability of detection at each sample unit, given presence, using our 8-visit protocol was estimated to be 0.98 (Royle et al., 2008).

We tested biologically meaningful univariate and multivariate candidate models (Burnham and Anderson, 2002). The models represent our best estimates of what is likely to be important to fishers at the landscape scale, based on the literature and our experience studying fishers in the field. As a starting point, we used conceptual models developed from a similar model-building exercise conducted for fishers in the southern Sierra Nevada (Spencer et al., in press). The original set of models was reviewed for their relevance to the Klamath region and the new prey-related models were added, resulting in a final set of 27 generalized model families (Appendix B). Within most model families was a set of closely related sub-models that generally varied slightly from one another.

We evaluated each model's fit to the data using the bias-corrected Akaike's Information Criteria (AIC_c) (Akaike, 1973). We used weighted model averaging for all models within 2 AIC units of the highest-ranked model. We calculated importance values for individual variables by summing the AIC_c weights for all models that contained the variable (Burnham and Anderson, 2002).

2.5. Spatial considerations

Intrasexual territoriality and limited dispersal should result in negative autocorrelation of fisher detections at distances less than a home range radius and positive autocorrelation at distances including >1 home range. Because sample units were deliberately spaced to avoid multiple samples per home range, we were interested primarily in the latter. We followed the method of Davis et al. (2007) and created a spatial autocovariate (SA) by weighting the data from sampling units within 10, 15, 20, 25, and 30 km of the reference sample unit by the inverse of the squared distance to the reference sampling unit, normalized by the sum of weights for all units in the distance region. We summed distance-weighted observations across all sample units in the neighborhood. We then added the SA to the best models (see below) to see if AIC_c values were influenced by its inclusion. The 25-km distance produced the best (SA-included) model; we used this weighting factor in all analyses. We compared AIC_c values for the top models with and without the SA. If a model that included the SA was better than the same model without the SA, we evaluated the correlation of their predicted probabilities of fisher presence to determine whether the SA should be included. If the correlation between the two models was >0.75, the SA variable was not included.

2.6. Model evaluation

We evaluated models first by integrating the area under the receiver operating characteristic curve (Area Under the Curve; AUC) to evaluate the classification skill of each model (Altman and Bland, 1994; Fielding and Bell, 1997). A model with no classification skill results in an AUC of ≤ 0.5 , whereas a perfect model (correctly predicting all detections and non-detections) would have an AUC of 1.0. We also tested each model using an independent data set consisting of track plate, camera or hair snare surveys (614 sample units) conducted in our study area from 1989 to 2007. These survey locations were not associated with our systematic surveys and were conducted by private or government biologists. One hundred and sixty-seven (27.2%) of the surveys were on private land. These data were highly clumped in distribution across the study area and, therefore, had spatial properties that differed from the model-building data set. To avoid spatial autocorrelation within the model-testing data set we applied a clustered point thinning procedure in ArcGIS with a cluster point tolerance of 5 km, which ensured that no two data points in the model-testing data set were < 5 km apart; a distance similar to the spacing in the original model-building data set. The thinning procedure resulted in the retention of 125 locations in the model-testing data set (collected from 1997 to 2007) which we overlaid on a map of the predicted probabilities of detection (from 0 to 1) derived from the best-fitting model. We calculated AUC and correct-classification rates based on the relationship of the test data survey results to the values predicted by the model.

We also used the probability of detection in each pixel to estimate the distribution and abundance of categories of varying predicted value (Boyce et al., 2002; Hirzel et al., 2006). We generated the “predicted to expected ratio”, P_i/E_i (Hirzel et al., 2006), as a measure of strength of selection. This index is < 1 when a probability class is selected against and > 1.0 when it is selected for; a value of 1 indicates no selection. A good model should show a monotonically increasing P/E curve. The index is sensitive to the number of probability classes chosen, so we used the moving window approach advocated by Hirzel et al. (2006). The P/E function served as an index of habitat selection and a measure of model calibration (Pearce and Ferrier, 2000). Although our final model predicts the probability of detection, we assume that areas with a higher probability of detection fulfill a greater number or quality of life-requisite needs for fishers and may therefore be used as an index of relative habitat suitability.

3. Results

3.1. The best-fitting model

We detected fishers at 37.9% (55/145) of the sample units (Fig. 1). Detections occurred across the study area, but most were in the central and southern portions (Fig. 1). The top ranking model included three variables: PHDWD (Percent Hardwood), INSOLINDEX (Insolation Index), and DFOR2 (Amount of Dense Forest) (Table 1). Three additional models were within 2 AIC_c units of the top-ranked model, and included the following variables in decreasing order of importance weights: Insolation Index, Amount of Dense Forest, Percent Hardwood, ADJ ELEV (Adjusted Elevation), MLFOR (Medium & Large Trees), STRUCT2 (Structurally Complex Forest), and MAMMPREY (Mammalian Prey) (see Appendix A for definitions) (Table 1).

We derived our final model by averaging the top four models proportional to their AIC_c weights. Using the model-building data set, and a cut-point in predicted value that best separates the detections from non-detections (0.35), this model had classification rates of 83.6% and 70.0% for detection and non-detection, respec-

tively (Fig. 2A). The AUC value for this averaged model was 0.858 and the Kappa value 0.504. Importance weights, for individual variables, indicated that Insolation Index, Amount of Dense Forest, and Percent Hardwood were most influential (Table 1).

Mammalian Prey, Structurally Complex Forest and Medium & Large Trees all have positive relationships with predicted value (Fig. 3). In contrast, Insolation Index appears to have a negative relationship suggesting that the more solar radiation a location receives the lower the predicted probability of detection. Percent Hardwood and Adjusted Elevation had quadratic response forms (Fig. 3).

A number of other variables that were not included in the final model, but which reflect structural or compositional aspects of the forest that are amenable to management were substantially different when their values at detection and non-detection sample units were compared (Appendix C). These included: HREPRO-AREAMN (Mean Patch Size of Suitable Reproductive Habitat), CWHR2-AREAMN (Mean Patch Size of Suitable Habitat), TS_RATIO (Ratio of Trees to Shrubs), BADHAB2 (Proportion with Poor Cover), LRGFOR (Proportion with Large-Diameter Trees) and SNOWDPTH (Maximum Mean Daily Snow Depth).

The 25-km radius neighborhood spatial autocorrelation model reduced the AIC_c value (i.e., improved the fit) only for the fourth highest-ranked model (Table 1). The correlation of predicted values of this model, with and without the spatial autocovariate, was very high ($r = 0.88$) indicating that including the spatial autocovariate would not improve predictive ability.

The final (averaged) model, when applied throughout the study area, produced a map with very heterogeneous predicted values (Fig. 4). Predicted probability of detection values in the eastern portion of the study area was generally lower, with the exception of a region in the east-central portion (northwestern Shasta and southwestern Siskiyou Counties). Areas with high habitat suitability values (> 0.60) were discontinuous, especially in the eastern portion of the study area. However, these areas, when considered together with the next highest habitat suitability class (0.40–0.59), appeared to retain considerable continuity from north to south in the western half of the study area (Fig. 4).

The final model was well calibrated, with the index of selection indicating negative values (selection against) for the lower predicted range (i.e., 0–0.40) and positive values for most of the range of higher probabilities (> 0.40 ; Fig. 5). Interestingly, the areas of lowest predicted probability were used much less than expected based on the area they represent in the study area, compared to the highest predicted probability areas (Fig. 5).

3.2. Test data

The 125 survey locations in the model-testing data set disproportionately occurred in the western and eastern margins of the study area (Fig. 4) and included 42 (33.6%) locations where fishers were detected. The best model varied substantially in its skill at predicting the results of these independent surveys. The AUC value for the test data was 0.676, indicating intermediate skill at classification. Using a threshold of 0.35 (the same value used for the original, model-building data set) resulted in 76.2% and 53.0% correct classification for detection and non-detection, respectively. Detections occurred more often in low predicted probability classes than non-detections occurred in high predicted probability classes (Fig. 2B); thus there were more errors of commission than omission.

3.3. Predicted probability of detection as a function of land ownership and allocation

Comparison of mean predicted probabilities of detection among land ownership and allocation categories revealed that public

Table 1
The four habitat models within two AIC units of the top-ranked model, ranked in decreasing order of model fit to the data. w refers to the AIC weight. Superscripts index the importance weight (Burnham and Anderson, 2002) and list the expanded name for each of the seven variables included in the 4 top-ranked models.

	Rank	Model	AIC _c	ΔAIC _c	w	Relative weight
1	PHDWD ^a	INSOL.INDEX ^b DFOR2 ^c	172.11	0.00	0.149	1.00
2	MAMMPREY ^d	INSOL.INDEX DFOR2 MLFOR ^e	172.61	0.50	0.116	1.29
3	PHDWD	INSOL.INDEX STRUCT2 ^f	173.00	0.89	0.096	1.56
4	ADJELEV ^g	INSOL.INDEX DFOR2	173.53	1.42	0.073	2.03

Variable importance weights:
^a Percent Hardwood = 0.552.
^b Insolation Index = 0.829.
^c Amount of Dense Forest = 0.616.
^d Mammalian Prey = 0.154.
^e Medium & Large Trees = 0.238.
^f Structurally Complex Forest = 0.160.
^g Adjusted Elevation = 0.248.

lands had higher mean values (0.397, SD=0.004) than private lands (0.292, SD=0.0017). Among the allocations of public land, Late-Successional Reserves had higher mean predicted values (0.488, SD=0.024) than congressionally reserved wilderness (0.384, SD=0.0026).

3.4. The best-fitting “biotic only” model

Our final model represents the average of the four top-ranked models (Table 1), each of which included 1 or more abiotic variables. Although this suggests that prediction is improved with a combi-

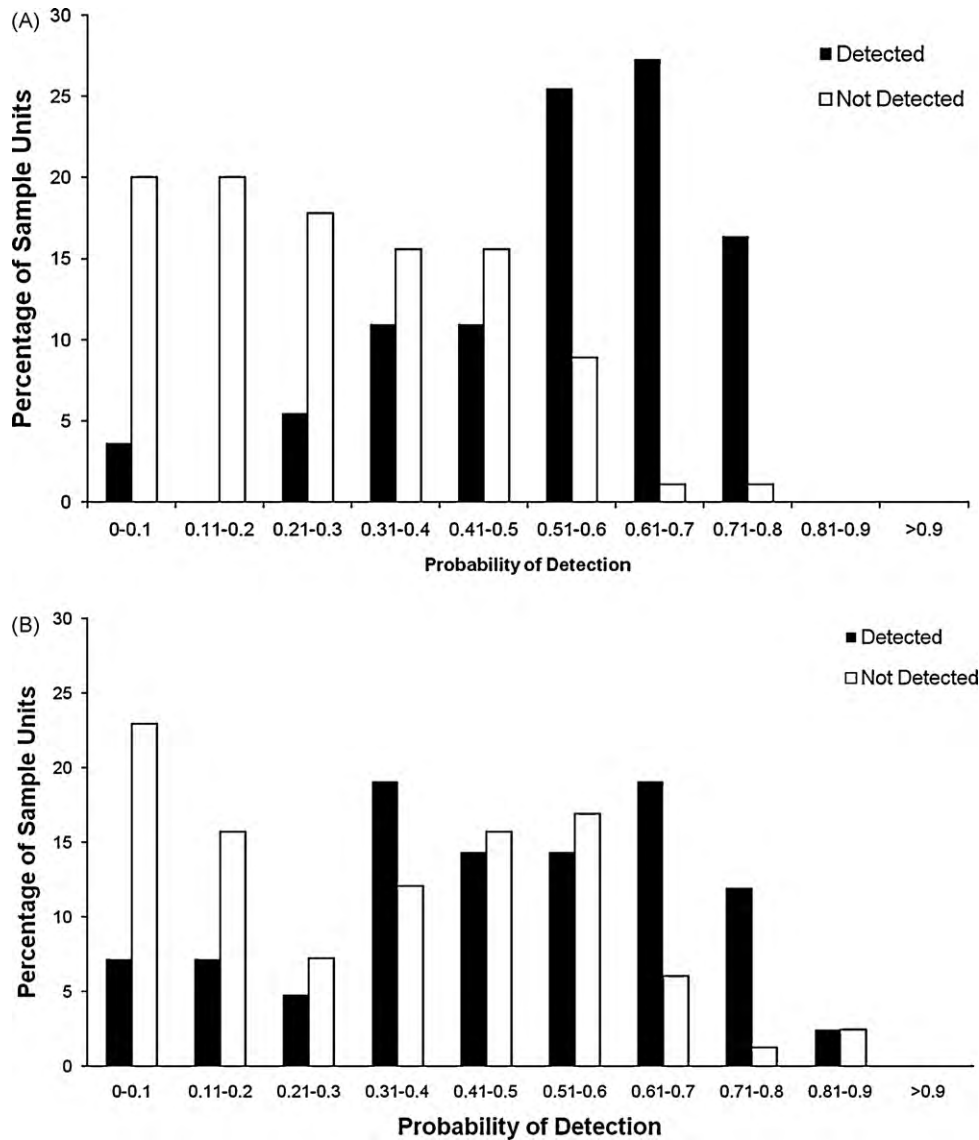


Fig. 2. The frequency distribution of sample units with detections and non-detections as a function of the predicted class of probability of detection for (A) the data used to build the model and (B) the data used to test the model.

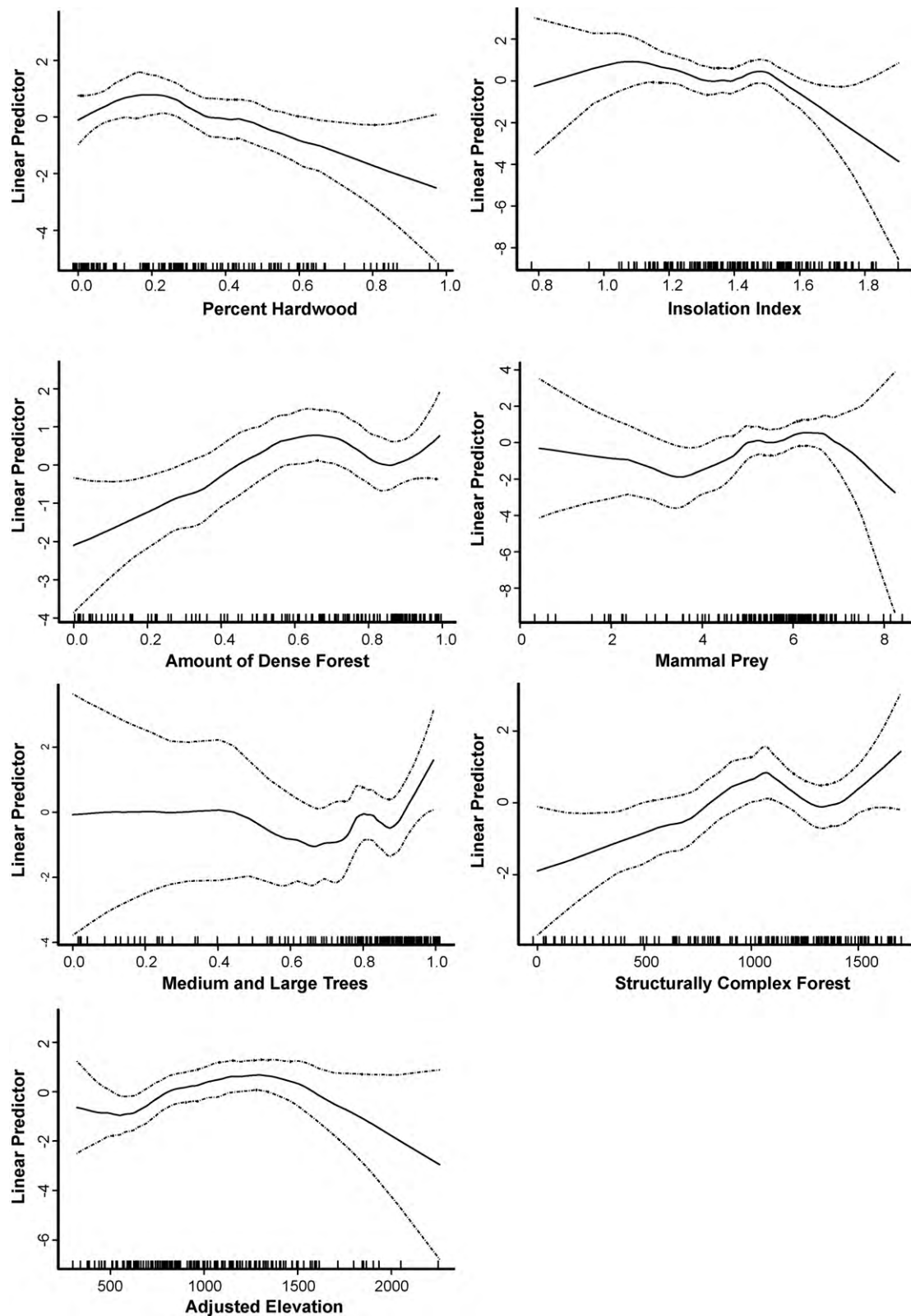


Fig. 3. Partial response curves for each of the variables in the top 4 top-ranked models. Response curves represent the relationship between the covariate and the predicted probability of detection, given the presence of the other variables in its respective model. Tick marks along the x-axis represent the distribution of the data. Response curves for variables that are in more than 1 of the 4 top-ranked models (e.g., Amount of Dense Forest; DFOR2) represent the variable's response in the highest-ranking model.

nation of biotic and abiotic variables, applying these models limits the opportunities that land managers have to alter landscapes to influence predicted habitat suitability for fishers because abiotic variables are beyond their influence. Thus, we also identified the

highest-ranking model that was comprised exclusively of biotic variables. This model included only Percent Hardwood (PHDWD) and Structurally Complex Forest (STRUCT2) and, although it ranked 23rd, it was only 5.28 AIC units lower than the highest-ranked com-

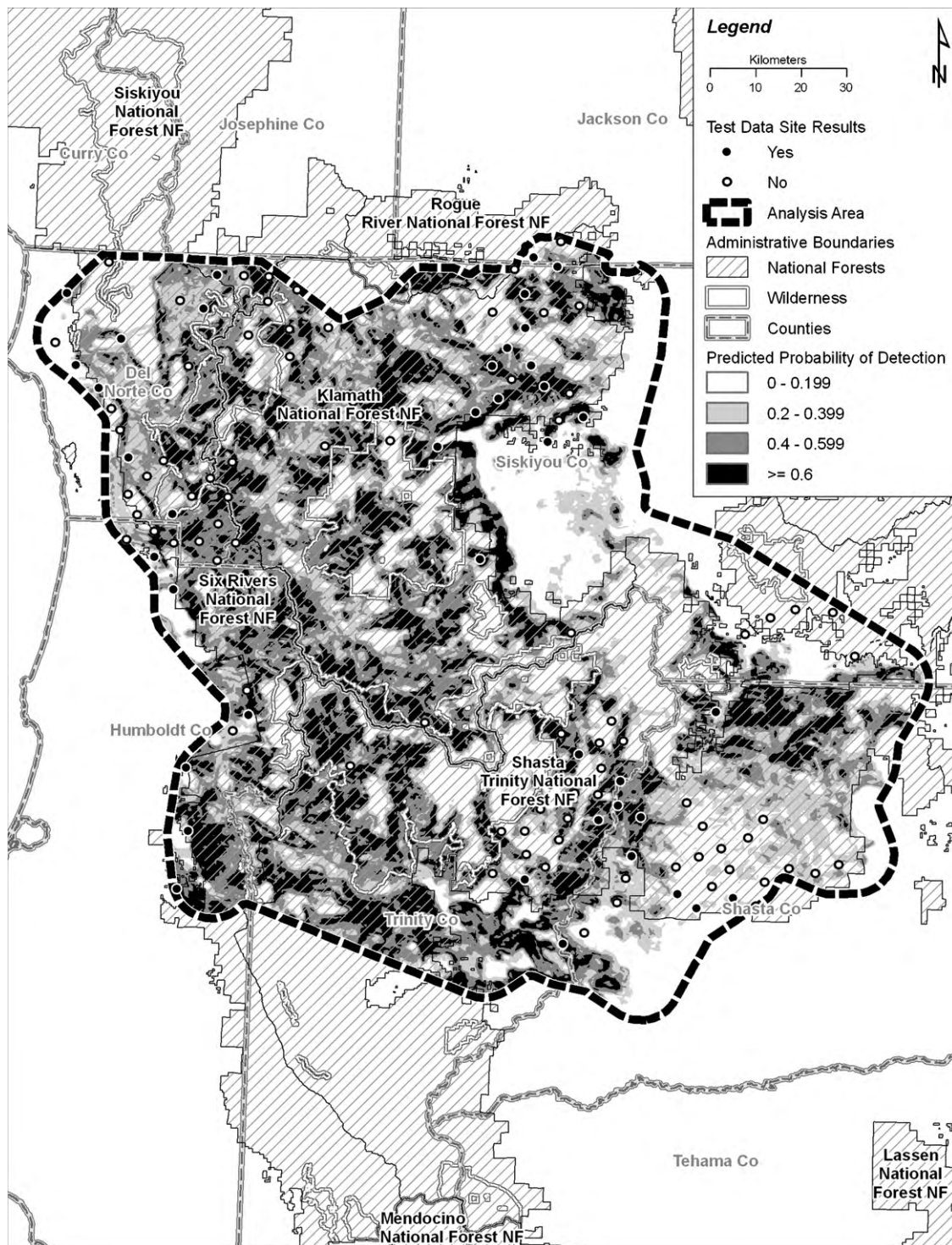


Fig. 4. Map of predicted probability of detection for fishers within the study area in interior northern California (dotted line). Each pixel in the base map is represented by 1 of the 4 detection-probability classes, based on the final model, which is an average of the 4 top-ranked models. The results of data used to test the model are represented by the circles; black circles represent sites where the test data confirmed the presence of a fisher and white circles represent test survey locations where a fisher was not detected.

bination model. The “biotic only” model also performed almost as well as our best-fitting model; a 0.35 probability cut-point resulted in correct-classification rates of 83.63% and 64.4% for fisher detection and non-detection, respectively.

4. Discussion

Our modeling exercise includes the widest breadth of potential predictors of any previous effort to model landscape-scale habi-

tat conditions for fishers. The spatial model identifies areas of important habitat within the Klamath province but also identifies important areas where connectivity may be limited between the Klamath Mountains and the Cascade Ranges and the Sierra Nevada to the southeast. Until now, a model built from local survey data in interior northern California has not been available to forest managers. Although we view the management application of the model as its most important function (see below), the variables included

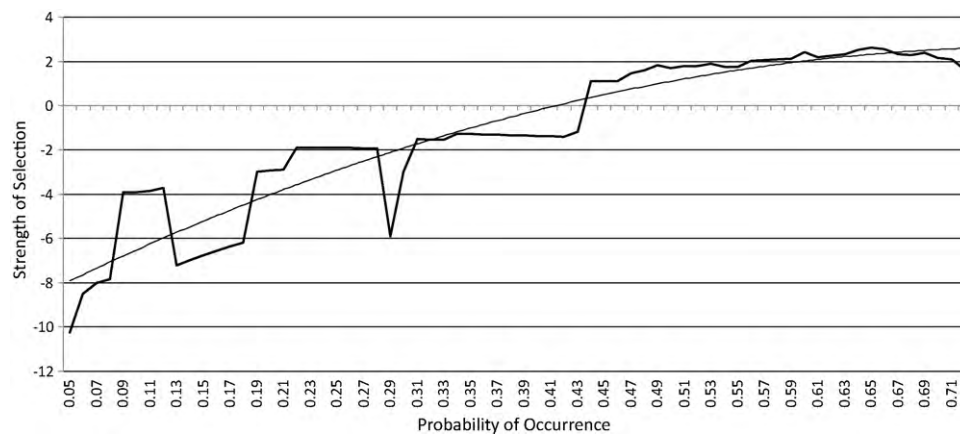


Fig. 5. The fitted regression line illustrates the relationship between the predicted probability of detection (from 0 to 1) and the strength of selection (Hirzel et al., 2006); the irregular line represents the actual data. This function evaluates the ability of our model to predict the detection of fishers in our interior northern California study area.

in the best-fitting model may help us to identify habitat characteristics that may limit fisher habitat suitability at the landscape scale. Many of the variables included in our final model represent characteristics frequently associated with descriptions of fisher habitat in western North America. In particular, dense structurally complex mixed hardwood/conifer forests, containing abundant large and medium-sized trees, have been identified as important habitat characteristics for fishers (Buskirk and Powell, 1994; Powell and Zielinski, 1994; Carroll et al., 1999; Buskirk and Zielinski, 2003; Weir and Harestad, 2003; Zielinski et al., 2004a,b; Davis et al., 2007; Purcell et al., 2009). The quadratic response forms of Percent Hardwood and Adjusted Elevation suggest that fishers typically occur in mixed hardwood-conifer forests and at intermediate elevations. The inclusion of elevation in the model probably reflects the selection of particular forests types, or elevations that do not have deep snowpack, a relationship that has been demonstrated elsewhere for fishers (Krohn et al., 1995, 1997) and for which we found a strong univariate relationship here as well (i.e., Maximum Mean Daily Snow Depth; SNOWDPTH in Appendix C).

Insolation Index, however, is a unique predictor among previous fisher models (but see Spencer et al., in press) and, given the negative relationship with predicted detection, is probably included in the model due to the generally reduced vertical and horizontal structure in less productive forests, or lower prey availability, at the hotter and drier topographic positions. Because Insolation Index had the highest importance weight among the covariates, we believe it warrants inclusion in future studies and additional consideration in fisher habitat planning. Climate change will likely interact with the effect of insolation on vegetation and topography, thus Insolation Index may be an important variable to monitor in the future.

Our research is the first to attempt to link fisher occurrence with prey metrics. The inclusion of a predictor based on potential availability of mammalian prey in the final model was somewhat surprising because fishers are dietary generalists (Zielinski et al., 1999) and have more complex spatial relations than species like the gray wolf (*Canis lupus*), whose distribution is strongly affected by the distribution of 1 or 2 key prey species (Mladenoff et al., 1995). Our mammalian prey indices, however, were created to represent the collective influence of all the mammalian prey that may be important in the fisher diet and, therefore, represented the composite importance of mammalian prey to a dietary generalist. Similarly derived indices of prey abundance have been useful at predicting the occurrence of goshawk (*Accipiter gentilis*), a forest raptor with multiple prey species (J. Dunk, Humboldt State University, unpubl. data). Our prey indices were an attempt to evaluate whether broad and coarse-scale data on the availability of habitat for mammal prey

would contribute to predicting fisher habitat suitability. We realize, however, that contributing to predictions is not the same as cause-and-effect. Nonetheless, we encourage subsequent researchers to consider these and other potential prey indices when evaluating fisher habitat.

The “biotic only” model included only two variables, both of which have been strongly associated with previous descriptions of fisher habitat: Structurally Complex Forest and Percent Hardwood. This model includes habitat characteristics that land managers can control and suggests that increasing the amount and distribution of structurally complex conifer forests, that also include a significant hardwood component, will contribute to the maintenance and/or restoration of fisher habitat in our study area. Also of note is the strong relationship of several other biotic variables with predicted probability of detection, in particular some descriptors of landscape configuration like Mean Patch Size of Suitable Habitat (CWHR2_AREAMN) and Proportion of Area with Poor Cover (BADHAB2) (Appendix C). These variables, together with the two variables in the biotic only model, can be manipulated by managers to favor the forest conditions where fishers tend to be detected.

Besides the obvious heterogeneous nature of the distribution of predicted habitat (Fig. 4), there was a pattern of higher habitat value in the western portion of the study area compared to the eastern portion. Carroll et al. (1999) found a similar pattern and speculated that it was probably due to the increased moisture and greater forest productivity and diversity in the western portion of the study area. Moreover, the eastern portion of the study area includes some large non-forested regions (i.e., grassland valleys) that reduce the amount and connectivity of potential fisher habitat. However, there is a distinct area of predicted high habitat suitability in the extreme east-central portion of the study area. Given its potential role as a “stepping stone” of suitable habitat between populations in north-western California and the Sierra Nevada, we believe this region should receive high priority for habitat conservation.

Our model, like all others, has limitations that make it “a simple approximation of the true probability surface” (Barry and Elith, 2006). The model did not perform particularly well when evaluated using the test data; especially in predicting locations where we would not expect fishers to be detected. Our model considered environmental information (for fishers and their mammalian prey) at a single scale (5 km²), and ignored potentially important variation occurring at other scales, especially the distribution of important microhabitat features (e.g., Zielinski et al., 2004a) and the distribution of potential competitors (Campbell, 2004). Missing covariates are a frequent source of unexplained variation in habitat models (Barry and Elith, 2006).

Moreover, compared to the survey data we used to build the model, the survey data we used to test it had considerably different spatial and temporal characteristics. The model-testing and model-building data sets were collected in different portions of the study area (compare locations of symbols in Figs. 1 and 4); in addition the model-building data were collected over a shorter period of time, and based on a random-based systematic sample, compared to the model-testing data. Nonetheless, if the landscape habitat features included in our final model explained most of the variation in fisher occurrence we would have expected the model to perform better when classifying the test data. Carroll et al. (1999) also tested their fisher landscape using independent data with different spatial and temporal characteristics, yet demonstrated better classification skill. The spatial extent of their model was more limited, however, than our larger and more heterogeneous study area and may explain why their test data were better classified.

Finally, classification skill in these types of associative models is not expected to be perfect, primarily because of source-sink population dynamics (Pulliam, 1988; Hanski, 1998). There are inherent limits to predictability, even in the simplest ecological settings (Melbourne and Hastings, 2009). We agree with Berglund et al. (2009) that a resource-based definition of habitat suitability must be stochastic and should allow for species to be absent from suitable habitat. If fishers are not in stochastic equilibrium with the environment, then we will not find fishers everywhere there is suitable habitat. The substantially better classification by the model of locations where fishers were detected (76.2%) than where they were not (53.0%) is consistent with this assumption. Also consistent are the results of our analysis of the strength of selection (Fig. 5) which indicated stronger avoidance of habitat conditions with low predicted value to fishers than selection for habitat with high predicted value.

4.1. Predicted occurrence as a function of land ownership and allocation

Public forest lands, which are managed for multiple values, had higher predicted value to fishers than private lands, which are generally managed for revenue from timber. Timber management on private land can be in conflict with the maintenance of structurally complex forests, so this result was not unexpected. Carroll et al. (1999) found a similar difference for their fisher landscape habitat model, which was developed for the region that overlaps the western portion of our study area. We found that public lands designated as Late-Successional Reserves (LSRs) had higher predicted value than lands designated as wilderness, a result also reported by Carroll et al. (1999). Because elevation influenced predicted habitat suitability in a quadratic fashion, the high-elevation forests where most wilderness areas occur were of lower value than the intermediate elevations where most LSRs occur. In addition, LSRs are more likely to include productive mixed conifer/hardwood forests characterized by large size class trees, and less deep snowpack, than high-elevation wilderness areas.

4.2. Applications

Whichever model managers apply, our final model or the biotic only model, we advocate its use at the appropriate scale for a number of potential applications which are described below and illustrated in Fig. 6.

4.2.1. Locating vegetation treatments, timber harvests, and rights-of-way

Managers of public and private forest lands are asked to prepare vegetation management plans that attempt to protect forests from the negative effects of wildfire and to propose timber harvests.

Similarly, plans for new public utilities and roads often require consideration of the effects on wildlife habitat value. Our map of the predicted probability of fisher detection (Fig. 4) provides important spatially explicit information, without which planners could unwittingly do significant damage to fisher habitat by proposing projects in areas of highest habitat value or in areas of potentially important habitat connectivity. Our mapped probability surface could be consulted during the planning process to determine whether the objectives of a project could be achieved by relocating it where it will have fewer adverse effects on fisher habitat suitability. An example of this occurred when the California Department of Transportation compared alternative routes for a realignment of Highway 101 with the predictions of Carroll et al.'s (1999) landscape habitat model (W. Zielinski, pers. obs.). Our model may also be useful for designing land purchases or exchanges, when the goal is to enhance the amount of fisher habitat or improving its connectivity.

4.2.2. Development of public-private conservation agreements

The Endangered Species Act enables the U.S. Fish and Wildlife Service to develop Candidate Conservation Agreements with Assurances (CCAA) with private landowners (U.S. Fish and Wildlife Service, 1999). A CCAA is developed with a landowner who may be able to provide a conservation benefit, and receive "assurances" to be protected from future regulations if the candidate species becomes listed. For example, our model could be used to identify the areas of greatest potential conservation benefit to the fisher and to negotiate reduced timber harvest in one area in exchange for increased harvest in other areas with lower conservation value.

4.2.3. Monitoring the abundance and distribution of fisher habitat

The model developed here is static, but includes variables that will change state over time; thus, results can and should be updated in the future. Thus, like models developed to track changes in stand or microsite habitat quality (e.g., Zielinski et al., 2006b), our landscape habitat model can be rerun with updated environmental data to yield new predictions. These can then be compared to previous predictions for the same region (e.g., "mean predicted value for Shasta County") to assess changes in fisher habitat conditions over time.

4.2.4. Reintroduction planning

Fishers have been reintroduced to a number of locations within their former range (R. Powell, North Carolina State University, unpubl. data) and habitat modeling is frequently used to choose among candidate areas for reintroduction (e.g., Lewis and Hayes, 2004). Currently, fishers appear to be relatively well distributed within our study area, but our empirically derived habitat map could be used to select appropriate locations live-trap fishers for reintroductions elsewhere.

4.2.5. Understanding patterns of habitat use

For any of the applications suggested above, the mean values of specific variables presented in Appendix C can assist management decisions. For example, in the CCAA example above (Section 4.2.2), we suggested a negotiated reduction in timber harvest in one area might exchange for increased harvest in another area with lower predicted habitat value to fishers. Target values can be developed for specific habitat variables (e.g., LRGFOR [Density of Large Trees]) to determine if monitoring guidelines contained in a formal agreement are being met.

4.2.6. Regional conservation planning

Spatially explicit results from landscape habitat models are often used to design reserves and other protected areas in large planning areas (Elith and Leathwick, 2009; Carroll et al., 2010). A

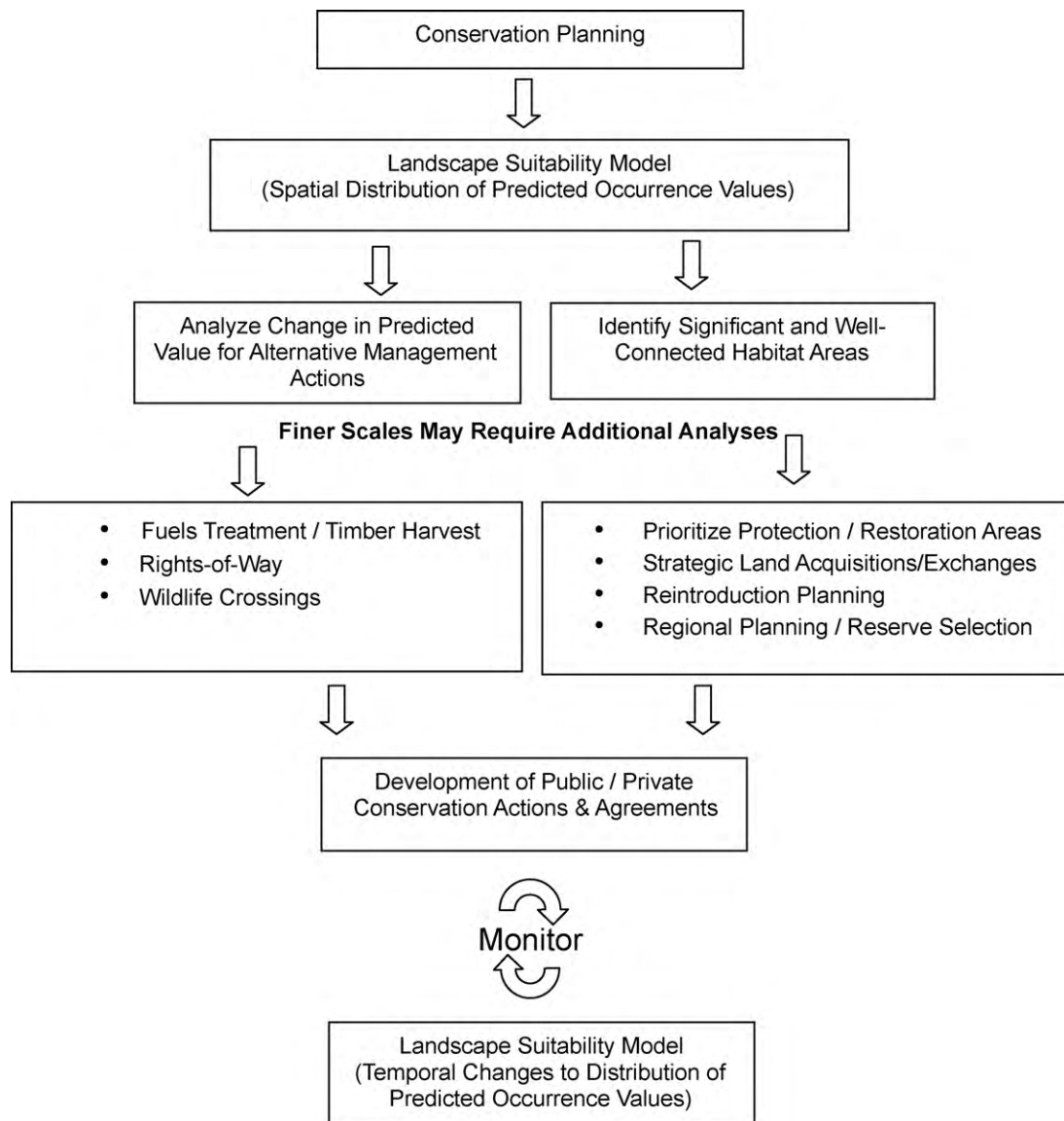


Fig. 6. Potential applications for the fisher habitat suitability model developed for the study area in interior northern California.

fisher landscape habitat model (Carroll et al., 1999) was used in combination with a similar model for the northern spotted owl (*Strix occidentalis caurina*) (Zabel et al., 2003) to evaluate how existing and proposed reserves protect predicted habitat value (Zielinski et al., 2006a). Our model could serve this same purpose if the designation of reserves becomes a priority in our study area.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.08.006.

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